# Roles of the Home Scar of *Collisella scabra* (Gould)

by

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*Abstract.* Most individuals of the prosobranch limpet species *Collisella scabra* (Gould, 1846) form a permanent home depression or home scar from which they forage. Laboratory experiments indicate that while on a scar, limpets are significantly less vulnerable to predation by *Pycnopodia helianthoides* (Asteroidea), *Pachygrapsus crassipes* (Crustacea), *Clinocottus* spp. (Pisces), *Octopus dofleini* (Cephalopoda), and *Freemania litoricola* (Turbellaria). A home scar effectively reduces predation by *Cancer antennarius* (Crustacea) only when limpets without home scars are more abundant than limpets on home scars. A home scar does not significantly reduce predation by *Pisaster ochraceus* (Asteroidea). Field work suggests that other roles of the home scar include a reduction in desiccation-induced mortality, as well as improved survival following sand burial. Limpets on home scars adhere to the rock more tightly than limpets off home scars.

## INTRODUCTION

MANY SPECIES of prosobranch and pulmonate limpets consistently return to the same site after their foraging activities (reviewed by UNDERWOOD, 1979, and BRANCH, 1981). Homing limpet species frequently form distinct substrate depressions called home scars. Usually a limpet will fit precisely into these depressions. LINDBERG & DWYER (1983) have shown that the home depression consists of two structural levels, an outer level that conforms to the shell margin and a central deeper depression that corresponds to the limpet's foot dimensions. It is important to distinguish homing behavior (site specificity) from scar formation because each can have several distinct roles, none of which are mutually exclusive. GARRITY & LEVINGS (1983) and LINDBERG & DWYER (1983) have reviewed the major hypotheses concerning the role of a home scar. A home scar can provide protection from biotic factors such as predation (BRANCH, 1975; VERMEIJ, 1978; COOK, 1980; WELLS, 1980; GARRITY & LEVINGS, 1983) and agonistic encounters from competitors (WRIGHT, 1977). A home scar also can provide protection from abiotic factors such as desiccation stress (FRETTER & GRAHAM, 1962; MCALISTER & FISHER, 1968; DAVIES, 1969; HA-

VEN, 1971; WOLCOTT, 1973; BRANCH, 1975; COOK, 1976; VERDERBER *et al.*, 1983; GARRITY, 1984), dislodgement by wave impact, and injury or dislodgement by sand scour (WOLCOTT, 1973).

These potential adaptive functions of home scars have been invoked widely, but there is little direct experimental evidence to support them (see BRANCH, 1981). In this paper we present evidence that the home scar of the prosobranch limpet *Collisella scabra* reduces predation rates for several predators. We also provide new evidence suggesting that the home scar reduces mortality induced by abiotic factors.

*Collisella scabra* (Gould, 1846) is found in the upper intertidal and splash zones on rocky shores of North America from the tip of Baja California to Cape Arago, Oregon (LINDBERG, 1981). This limpet has been well studied (reviewed by ABBOTT & HADERLIE, 1980), and its ability to home and form home scars is well documented (HEWATT, 1940; VILLEE & GROODY, 1940; BRANT, 1950; JESSEE, 1968; LINDBERG & DWYER, 1983). The natural predators of limpets include several species of small mammals, birds, fish, seastars, crabs, mollusks, and flatworms (reviewed by WELLS, 1980, and BRANCH, 1981).

## Table 1

Predators used in laboratory feeding experiments, including numbers and sizes used. Sizes of limpets offered to each predator are also indicated.

| Species | Number of predators | Size of predators | Limpet size (mm) |
|---|---|---|---|
| *Pisaster ochraceus* | 4 | 11 cm, arm length 8 cm, arm circumference | 15–20 |
| *Pycnopodia helianthoides* | 1 | 20 cm, diameter | 15–20 |
| *Pachygrapsus crassipes* | 4 | 3 cm, carapace width 2.5 cm, chelae length | 15–20 |
| *Cancer antennarius* | 4 | 9 cm, carapace width 3.5 cm, chelae length | 12–23 |
| *Freemania litoricola* | 5 | 2 cm, length | <10 |
| *Clinocottus* spp. | 6 | 8 cm, standard length | 10–15 |
| *Octopus dofleini* | 1 | 15 cm, arm length | 10–15 |

Specifically, this study focused on the following predators of *Collisella scabra*: *Pisaster ochraceus* Brandt, 1835 (Asteroidea), *Pycnopodia helianthoides* Brandt, 1835 (Asteroidea), *Pachygrapsus crassipes* Randall, 1839 (Crustacea), *Cancer antennarius* Stimpson, 1856 (Crustacea), *Freemania litoricola* (Heath & McGregor, 1912) (Turbellaria), *Octopus dofleini* Wülker, 1910 (Cephalopoda), *Clinocottus recalvus* Girard, 1857 (Pisces), and *Clinocottus analis* (Girard) (Pisces).

## MATERIALS AND METHODS

### Laboratory Predation Experiments

*Collisella scabra* and predators were collected during spring 1983 from rocky sites located on, or adjacent to, the Bodega Marine Laboratory Reserve (Sonoma Co., California). Rocks containing *C. scabra* on home scars were brought directly into the laboratory. Limpets that were to be offered without home scars to predators were gently pried off field rocks with a small spatula. These limpets were allowed to attach to rocks, but lacked home scars. Animals were maintained in aquaria coupled to a flow-through seawater system. Predators were starved for 48 h prior to the start of an experiment, and experiments were conducted within 3 days of animal collection.

For each experiment three to six rocks were situated on the bottom of a flow-through aquarium. On the rocks were 10 pairs of *Collisella scabra*; for each limpet with a home scar there was one limpet without a home scar. To eliminate handling bias, each limpet on a home scar was removed with a spatula (in the same way as limpets with-

out home scars) and then returned to its home scar. *Collisella scabra* individuals, with and without scars, were distinguished from each other by small lines or dots of paint applied to the top of each shell. Specific predators were introduced into each aquarium, and the experiments were run for 3 days. To keep the number of *C. scabra* constant, aquaria were checked every 12 h for consumed limpets; consumed limpets were replaced. Limpets with home scars were replaced by adding rocks with the appropriate number of limpets on home scars. The procedure was changed for the experiment involving *Freemania*. The lower feeding activity of these flatworms necessitated longer trials; this experiment ran for 23 days and 5 pairs of limpets were used in each trial.

The number of predators and predator size varied for each experiment (Table 1). Preliminary studies and literature sources were used to determine the range of limpet sizes offered to each predator (Table 1).

### Behavioral Observations

*Collisella scabra* with home scars may be consumed while on scars or when off (*e.g.*, while foraging). The laboratory predation experiments did not discriminate between these alternatives. In order to obtain a better understanding of the predation process, seastar and crab predators were observed directly during the feeding experiments. Because crabs feed primarily at night, they were observed by using a red light. All other observations took place during the day. An additional set of observations was made on *Cancer* crabs that were offered 20 limpets without home scars (instead of 10) and 10 limpets with home scars.

### Field Experiments

A field study was conducted to assess the differential survival of *Collisella scabra* individuals with and without home scars. Two experimental plots were established on exposed, rocky surfaces. In a 2 × 1.5-m plot, 101 *C. scabra* were removed, marked, and replaced on their home scars. An equal number of *C. scabra* were removed from another location, marked, and positioned next to the limpets located on home scars. In order to control for emigration, a second plot, 2 × 1 m, was outlined with Tanglefoot® to prevent limpet movement out of the plot. In this plot, 53 limpets with scars and 53 limpets without scars were handled in the same way as limpets in the first plot. After 8 days, the number of remaining *C. scabra* individuals with and without home scars was determined. This experiment was repeated 2 wk later at the same sites with 103 pairs of limpets in the first plot and 45 pairs of limpets in the plot outlined with Tanglefoot. During the first experiment, low tides occurred at midday during a week of unusually hot and sunny weather. The second experiment was run during a more typical week of early morning tides and cool, cloudy weather. Exposure and intertidal height (+1.6 m above MLLW) of the two sites were

## Table 2

Numbers of *Collisella scabra* consumed during predation experiments.

| Predator | Total | With-out scar | With scar | G | P |
|---|---|---|---|---|---|
| *Pisaster ochraceus* | 73 | 42 | 31 | 1.67 | >0.10 |
| *Pycnopodia helianthoides* | 66 | 47 | 19 | 12.26 | <0.001 |
| *Pachygrapsus crassipes* | 29 | 21 | 8 | 6.04 | <0.025 |
| *Cancer antennarius* | 60 | 36 | 24 | 2.41 | >0.5 |
| *Freemania litoricola* | 10 | 8 | 2 | 3.86 | <0.05 |
| *Clinocottus* spp. | 21 | 18 | 3 | 11.88 | <0.001 |
| *Octopus dofleini* | 4 | 4 | 0 | 4.92 | <0.05 |

comparable except the site without Tanglefoot contained horizontal and vertical surfaces; the site with Tanglefoot consisted of only horizontal surfaces.

## RESULTS

### Laboratory Predation Experiments

The importance of a home scar in reducing predation depended on the predator species. Based on a G-test (William's correction when n < 10) (Table 2), *Pycnopodia*, *Pachygrapsus*, *Freemania*, *Octopus*, and *Clinocottus* consumed significantly more *Collisella scabra* without a home scar than *C. scabra* with a home scar. The results for *Cancer* and *Pisaster* were not statistically significant, but more predation on *C. scabra* without home scars did occur.

### Behavioral Observations

*Pycnopodia*. *Pycnopodia* covered an entire rock while it was feeding, so ingestion could not be observed directly.

The *Pycnopodia* moved over each of 6 rocks, stopping for 5 to 10 min on each. After 45 min all but one of the limpets without a home scar were eaten, but no limpets on scars were eaten (Table 3). After 1.5 h the seastar became active again, but it passed over rocks on which there were limpets on home scars. At one point, however, the seastar moved onto a section of a rock where 2 of 3 limpets possessing home scars were not in their scars. When the seastar left the rock after 10 min, both limpets that had been off of their home scars had been consumed. The seastar continued to move over the rocks within the aquarium and did not feed on any *Collisella scabra* individuals located on home scars, but consumed the last limpet that was without a home scar.

*Pisaster*. After the tube feet of a *Pisaster* encountered a limpet, the seastar would move in the limpet's direction and cover it for about 10 min. *Pisaster* did not seem to distinguish between limpets on or off of home scars; numbers of limpets consumed and handling time were not substantially different for limpets on or off home scars (Table 3).

*Pachygrapsus*. Frequently, *Pachygrapsus* would touch limpets with its legs or chelipeds. On several occasions a crab would sit for up to 5 min in front of a limpet without touching it. Other times, a crab quickly would touch a limpet with a claw. Crabs attacked limpets by grasping a limpet shell with a cheliped. If the limpet was removed, it was held with one cheliped while the limpet flesh was removed with the other. The crabs frequently switched the limpet from one claw to the other.

*Pachygrapsus* was never observed removing a *Collisella scabra* from a home scar, but frequently tried to do so. Usually a crab would try for 1 or 2 sec, but attempts occasionally lasted up to 60 sec. For limpets not on home scars, crabs never required more than 5 to 10 sec to remove the limpet from the substrate (Table 3).

## Table 3

Summary of predator behavioral observations. Predators were offered 10 limpets with home scars and 10 limpets without home scars, except for the second *Cancer* observation period. Twenty limpets without home scars were used in that second trial.

| Predator | Observation period | Number limpets consumed | | | Handling time (min) | |
|---|---|---|---|---|---|---|
| | | With scars | | No scar | On scar | Off scar |
| | | On | Off | | | |
| *Pisaster ochraceus* | 1400–1730 hours (210 min) | 4 | 1 | 7 | 10–15 | 10–15 |
| *Pycnopodia helianthoides* | 1400–1730 hours (210 min) | 0 | 2 | 10 | 5–10* | 5–10 |
| *Pachygrapsus crassipes* | 0000–0600 hours (360 min) | 0 | 2 | 3 | 0.08–1* | 0.08–0.17 |
| *Cancer antennarius* | 0000–0600 hours (360 min) | 4 | 4 | 10 | 0.5–10 | 0.05–0.08 |
| | | 2 | 2 | 15 | up to 0.5 | 0.05–0.08 |

* Unsuccessful attempts.

Table 4

Numbers of *Collisella scabra* missing from field plots after eight days.

| Number of missing limpets | Experimental plot (no Tanglefoot) | | Control plot (Tanglefoot) | |
|---|---|---|---|---|
| | Sunny/hot period n = 101 | Cloudy/ cool period n = 103 | Sunny/hot period n = 53 | Cloudy/ cool period n = 45 |
| With home scars | 12 (14%) | 3 (3%) | 8 (15%) | 2 (4%) |
| Without home scars | 46 (45%) | 26 (25%) | 45 (85%) | 15 (33%) |

*Cancer.* These crabs appeared to search actively for limpets. Crabs repeatedly spread their chelipeds, and took a step forward while bringing their chelipeds close together anteriorly. After a *Cancer* encountered a limpet with its chelae, the crab would try to remove it by squeezing the limpet between a chela and pulling it off the rocks. The crabs used both claws for feeding. The shell was crushed and the flesh pulled out using the maxillipeds. One dominant *Cancer* individual consumed 75% of the limpets ingested. Two of the four crabs ate no limpets.

Limpets with and without home scars were consumed by *Cancer,* but the handling time was longer for limpets in scars (up to 10 min compared with about 0.08 to 0.17 min). Crabs always were successful in removing limpets without home scars, but would frequently be unsuccessful if a limpet was on a scar (Table 3). Crabs seemed to remember the location of limpets and would return to try again if another limpet was not quickly encountered. During the second observation period, the crabs were placed in an aquarium containing 10 limpets within scars and 20 (instead of 10) limpets without scars. During this period, the time spent attacking limpets on scars decreased after crabs encountered several limpets without scars. Subsequent attacks on limpets on scars were rare.

### Field Experiments

A survey of the experimental plots after 8 days indicated that more limpets without home scars were missing from the plots than limpets with home scars. For both the sunny, hot period and the cloudy, cool period, greater numbers of scar-denied limpets were missing from both the Tanglefoot plots ($\chi^2 = 24.4$, $P < 0.05$; $\chi^2 = 8.5$, $P < 0.05$) and the non-Tanglefoot plots ($\chi^2 = 18.8$, $P < 0.05$; $\chi^2 = 16.7$, $P < 0.05$). The relative loss of limpets with and without home scars was higher in the Tanglefoot plots for each trial. Mortality was greater for limpets both with and without home scars during the sunny, hot period when compared to mortality during the cloudy, cooler period (Table 4).

### DISCUSSION

Behavioral observations and the results of the laboratory experiments indicate that the effectiveness of a home scar in the reduction of predation depends on the predatory species. Possession of a home scar effectively reduced predation by the seastar *Pycnopodia*. Behavioral observations suggest that limpets with home scars were consumed only when they were off their scars foraging. In nature *Collisella scabra* lives higher in the intertidal zone than *Pycnopodia*, and their distributions rarely overlap. WELLS (1980) has shown that *C. scabra* forages only while awash; during high tide limpets remain on their home scars. The possession of a home scar (coupled with the above mentioned activity pattern) appears to be an effective predation avoidance mechanism.

*Pachygrapsus* is another predator that cannot prey as effectively on limpets on home scars. CHAPIN (1968) suggests that one method by which a *Pachygrapsus* attacks a limpet is by prying the limpet off a rock using a cheliped. However, Chapin notes that this method is effective only if the limpet does not have its shell clamped to the substrate; the crab must be able to get underneath the shell edge. A home scar eliminates this mode of attack. Behavioral observations suggest that *Pachygrapsus* also removes limpets by pinching the top of the shell and pulling. This was never successful when a limpet was on a home scar, but took only 5 to 10 sec when limpets were not on scars.

In contrast to *Pachygrapsus, Cancer antennarius* are able to prey upon *Collisella scabra* on home scars. The specimens of *Cancer* used in this study were larger and presumably stronger than those of *Pachygrapsus. Cancer* was never observed prying limpets off the rocks; instead it grasps limpet shells with a cheliped and pulls. Behavioral observations indicate that limpets without home scars are removed from rocks much more quickly than limpets with home scars (0.05–0.08 min *versus* 0.5–10 min). The number of attempts and the amount of time crabs spent attacking limpets on scars decreased when the proportion of limpets without home scars was increased. In nature one might expect a home scar to reduce predation rates on *C. scabra* because other gastropod species without home scars (or escape responses) presumably would represent a food resource with a shorter handling time.

*Freemania* may be a significant predator on *Collisella scabra. Freemania* and *C. scabra* do overlap in their intertidal distributions, although *C. scabra* is characteristically found higher than *Freemania* (PHILLIPS & CHIARAPPA, 1980). PHILLIPS & CHIARAPPA (1980) suggest that the snug fit of *C. scabra* in its home scar may reduce the probability that a limpet would be detected by a foraging flatworm, and if detected, successfully engulfed. In this study fewer limpets with home scars were consumed by *Freemania.*

WELLS (1980) showed that the home scar of *Collisella scabra* reduces the rate of predation by *Octopus bimaculatus*

(Verrill) and *Octopus bimaculoides* (Pickford & Mc-Connaughey) in the laboratory. Wells reports that twice as much time was required for *Octopus* spp. to consume all of the limpets with home scars as was required to consume limpets without scars. The results of the present study provide further evidence that a home scar reduces predation by *Octopus* spp.

The home scar also effectively reduces predation by the sculpins *Clinocottus recalvus* and *Clinocottus analis*. The ability of a home scar to reduce fish predation was demonstrated experimentally for the pulmonate limpet *Siphonaria gigas* by GARRITY & LEVINGS (1983). Their experiments and observations on a pulmonate limpet agree with those of this study on a prosobranch limpet. Fish commonly forage for limpets in the intertidal zone, and limpets off their scars are quite vulnerable. Both *S. gigas* and *Collisella scabra* further reduce predation by remaining on their home scars during the most active fish feeding period (GARRITY & LEVINGS, 1983; WELLS, 1980).

In contrast to the other predators used in this study, *Pisaster* does not appear to distinguish between limpets on or off home scars. FEDER (1963) found that *Collisella scabra* is the most abundant limpet in the diet of *Pisaster*, even though the overlap of distributions of the seastar and *C. scabra* is minimal. GARRITY & LEVINGS (1983) report that home scars afford no protection for *Siphonaria gigas* from the seastar *Heliaster microbrachius*, but state this seastar is extremely uncommon.

The field experiments clearly indicate the survival value of a home scar for *Collisella scabra*. Limpets on home scars consistently exhibited higher survival than limpets without scars. One probable reason for enhanced survival is that home scars help reduce desiccation-related mortality. In both plots, mortality rates were higher during the hot and sunny experimental period than during the cool and cloudy experimental period. WOLCOTT (1973) reported that when individuals of *C. scabra* were placed on smooth surfaces, limpets with smooth shell margins had significantly lower desiccation rates than limpets with rough margins. This situation is analogous to limpets with and without home scars. Several studies have found that a home scar helps emerged limpets reduce water loss, and thus reduce desiccation-related mortality. This has been demonstrated for prosobranch (GARRITY, 1984) and pulmonate limpets (MCALISTER & FISHER, 1968; VERDERBER *et al.*, 1983). However, GARRITY (1984) found that although possession of a home scar resulted in a significant reduction in water loss for both *Siphonaria maura* and *Siphonaria gigas*, there was no significant difference in mortality between limpets on and off scars.

VERDERBER *et al.* (1983) present laboratory and field data that suggest that if *Siphonaria alternata* individuals are denied home scars they desiccate, causing a loss of muscular control, and become increasingly vulnerable to both predators and waves. Thus, *Siphonaria* may suffer mortality directly and indirectly due to desiccation effects.

This possibly was the situation in the current study. Visual examination of scar-less limpets during the sunny period revealed that almost all were desiccated and limpets were easy to pry manually off the substrate.

A priori, one would expect more scar-less limpets to have disappeared from the field plot without Tanglefoot because limpets could emigrate and benthic predators immigrate. However, in this study limpet disappearance was higher in the plot with Tanglefoot. Perhaps this is because the site outlined with Tanglefoot did not contain vertical surfaces while the Tanglefoot-free plot contained both horizontal and vertical surfaces. Limpets on vertical surfaces would be less vulnerable to predation by birds (Lindberg, personal communication; FRANK, 1982) and possibly desiccation stress (HAVEN, 1971). Unfortunately, limpet disappearance as a function of surface orientation was not noted in this study.

Another home-scar function was suggested in the spring of 1980, when one of us (V. Connor) had a study site that suddenly was covered with 2–3 m of sand. Before the sand appearance, the site contained large populations of *Collisella scabra* and another limpet *Collisella digitalis* (Rathke, 1833). After two months, sand levels were low enough to recensus the populations. Nearly all of the *C. scabra* (80%) had survived, but most of the *C. digitalis* (80%) had disappeared. As both species can survive starvation for this amount of time, one possible explanation for this observation is that the limpets with home scars can better resist the deleterious effects of sand burial than can limpets without home scars, such as *C. digitalis*.

An additional role of the home scar of *Collisella scabra* not examined in this study has been suggested by WRIGHT (1977). A home scar allows individual *C. scabra* to inhabit areas near the larger agonistic limpet *Lottia gigantea* Sowerby, 1834. The home scar prevents *C. scabra* from being pushed off the substrate by the aggressive *Lottia*.

The results of this and other studies indicate that it is more difficult to dislodge a limpet while it is on a home scar. This is in part due to the absence of a space between the shell margin and the substrate, but may also be due to an increase in the tenacity exhibited by limpets on home scars. Connor (in preparation) found that the shear force required to dislodge a stationary *Collisella scabra* from a home scar always exceeded 5.0 kg/cm², while only 2–3.5 kg/cm² were required to remove scar-denied limpets. Similar values were reported by Wright (in BRANCH, 1981: 348). This increase in tenacity exhibited by limpets on home scars may be an additional reason why a home scar provides protection from predators. It also may play a role in preventing dislodgement by wave forces, but under normal conditions this is probably not as significant. Other limpet species co-occur with *C. scabra* and typically exhibit tenacity values similar to scar-denied *C. scabra* (Connor, unpublished data).

The formation of home scars is cited most often as a mechanism to minimize desiccation and associated effects.

However, it also frequently is inferred that the primary role is not to prevent desiccation, but rather to prevent dislodgement (WOLCOTT, 1973). This idea is supported by the fact that subtidal species and intertidal species inhabiting tide pools also form home scars, even though there is little threat of desiccation (LINDBERG & DWYER, 1983). BRANCH (1975) suggests that home scars serve different functions in different species, including both predation and desiccation resistance. This is supported for both prosobranchs and pulmonates by the studies presenting direct evidence for home scar function. WELLS (1980), studying *Collisella scabra*, and GARRITY & LEVINGS (1983), studying *Siphonaria gigas*, propose that home scars serve to reduce predation. VERDERBERGER *et al.* (1983), studying *Siphonaria alternata*, and GARRITY (1984), studying *Scurria stipulata*, suggest that home scars serve to reduce desiccation. However, there is no reason for assuming the exclusivity or primacy of any one function or that home scars serve the same roles in both prosobranch and pulmonate limpets. In this study, the home scar of *C. scabra* simultaneously affords protection against many factors. The multiple roles of a home scar occur simultaneously because the mechanisms by which scars afford protection appear to be the same. Higher tenacity while in the home scar increases the force necessary to dislodge a limpet by any force, including predators, competitors, or wave shock. The close fit of the shell margin to the substrate reduces rates of water loss and the effectiveness of predators that need to get under the shell, as well as protecting vulnerable tissue from injury by moving sand particles and predators.

We suggest that the home scar has no single role in *Collisella scabra,* but rather serves to protect this limpet from a variety of factors that an individual limpet may encounter during its lifetime.

## ACKNOWLEDGMENTS

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